# *The Inorganic Nutrition of Loblolly Pine And Virginia Pine With Special Reference To Nitrogen and Phosphorus*

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FOREST TREES, and particularly pines, generally are considered to be able to grow when supplied with relatively low amounts of mineral nutrients. Pines often invade land abandoned when it is too poor for further agricultural use. This invasion is especially characteristic of loblolly pine (*Pinus taeda* L.) and Virginia pine (*P. virginiana* Mill.) In fact, a common name of loblolly pine, old-field pine, is based on its habit of becoming established on abandoned fields. Virginia pine is also frequently found on road fills and cuts and on eroded lands as well as on naturally thin, poor soils. Little information exists, however, concerning the level of nutrients at which these pines will grow and their responses to increased amounts of nutrients.

There have been few studies of the nutrition of forest trees with nutrient or sand culture, and only two concerned with loblolly pine.[1] Addoms (1937) grew loblolly pine in nutrient culture with nitrogen at levels of 136 and 156 ppm and phosphorus at 146 and 198 ppm. for 29 months and obtained good growth of the trees. This appears to be the only report of culture studies concerning nitrogen and phosphorus nutrition with this species. Davis (1949) employed nutrient solutions to study the effect of calcium level on the development of loblolly pine. He noted that at 2 to 5 ppm of calcium, in contrast to 200 ppm, terminal buds were smaller, mitotic figures were smaller, needles were smaller in cross section with fewer and smaller cells, and

[1]Since this was written the authors have seen the article by Woodwell who found the optimum range of nitrogen and phosphorus for loblolly pine to be 75 to 600 ppm and 40 to 600 ppm, respectively. See Woodwell, G. M. Factors controlling growth of pond pine seedlings in organic soils of the Carolinas. Ecol. Monographs 28: 219-236. 1958.

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root tips were more blunt and rounded.

Empirical evidence of the effects of fertilization on the growth and development of many species of forest trees helps in estimating requirements for any one species. In a nursery fertilization study, Switzer and Nelson (1956) noted that the dry weights of loblolly pine seedlings varied only with changes in the amount of nitrogen added as fertilizer. Nitrogen concentration in the foliage was 1.33 percent when no fertilizer was added and 1.59 percent when nitrogen was added at the rate of 300 pounds per acre. The phosphorus concentration of the needles was 0.19 percent with no amendments and 0.18 percent when phosphorus was added at the rate of 300 pounds of phosphate, calculated as $P_2O_5$, per acre. According to Young (1948) in Australia, increasing the soil phosphate (the $P_2O_5$) up to 146 ppm resulted in increased growth of loblolly pine valued as equal to the cost of the fertilizer. The phosphate concentration of the needles ranged from 0.145 percent to 0.319 percent after phosphate was added at rates of 36 to 281 ppm.

In another study in Australia, Richards (1956) reported that a minimum total $P_2O_5$ phosphate content of 135 ppm in the surface soil is required for healthy growth of loblolly pine and that the optimum concentration appeared to be about 210 ppm. Maki (1955) fertilized 6-, 9-, 12-, and 16-year-old plantations of loblolly pine with nitrogen at rates of 0, 80, and 160 pounds per acre and with phosphate at rates of 0, 40, and 80 pounds per acre. After 3 years, growth in diameter was significantly greater in the nitrogen fertilized trees than in the unfertilized trees. He observed no significant response to phosphorus.

No reports concerning the reponse of Virginia pine to any nutrients have been published.

Information from studies with other conifers is of additional assistance in evaluating the nutritional requirements of loblolly and Virginia pines. In a sand culture study of the requirements of eastern white pine (*Pinus strobus* L.), Mitchell (1939) found that the deficiency level for nitrogen and phosphorus was 0 to 50 ppm for both elements, and the optimum range was 50 to 200 ppm for both elements. The toxic level of nitrogen was 350 ppm or more, and of phosphorus 400 ppm or more. Hobbs (1944) recorded the deficiency symptoms of white pine, shortleaf pine (*P. echinata* Mill.), red pine (*P. resinosa* Ait.) and pitch pine (*P. rigida* Mill.) when grown in sand culture without nitrogen and without phosphorus. Nitrogen deficient trees were pale green. Trees deficient in phosphorus showed necrosis of the lower needles, which sometimes developed a purplish red color before becoming necrotic. Western redcedar (*Thuja plicata* Donn.) showed definite response to nitrogen and to phosphorus in pot culture tests, according to Gessel *et al.* (1950).

In plantations and natural stands, nitrogen appears to increase diameter growth. Tamm (1956) observed that in 30-year-old Scotch pine (*Pinus sylvestris* L.) plantations fertilized with nitrogen at rates of 0, 50, 100, and 200 kg per hectare, the increased growth leveled off between 100 and 200 kg per hectare. Best diameter growth was related to a foliage content of 2.0 to 2.5 percent. Gessel and Shareaft (1957) found that the diameter growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) increased during a 5-year period after a total of 350 pounds of nitrogen was applied per acre.

Phosphate fertilizers have also been found to increase growth of trees in plantations and in natural stands. For example, according to Kessel and Stoate (1938) in Australia, *Pinus pinaster* Ait. attained an average height of 27 feet in 11 years as a result of applications of 100 pounds of superphosphate per acre at 2- to 3-year intervals. Unfertilized stands stagnated at 3 to 5 feet. Barnes and Ralston (1953) increased the height of slash pine (*P. elli-*

*ottii* Engelm.) with 1–2 tons of phosphate per acre. Planted spruce in Germany grew significantly more in height when it was fertilized with phosphate at the rate of 60 kilograms of phosphorus, as $P_2O_5$, per hectare (Attenberger, 1956).

There is an increasing amount of data describing the nutrient content of forest tree foliage on various soils and following fertilization. Analysis of the foliage of plants for an indication of the nutritional level of soil is widely accepted. Goodall and Gregory (1947) reviewed the status of foliar plant analysis and pointed out the superiority of the technique over soil analysis as a guide to plant requirements. Ulrich (1952) has also reviewed the more recent progress in this approach to soil and plant needs.

The nitrogen concentration of Douglas-fir needles ranged from 0.91 percent in shallow gravelly soils to 2.1 percent in deep loam (Gessel and Walker, 1956). In one experiment the nitrogen content of the needles increased from 1.17 percent to 2.45 percent after 280 pounds of ammonium nitrate and 320 pounds of ammonium sulfate were applied per acre. Roth and Copeland (1957) found an increase in the nitrogen content of shortleaf pine needles after nitrogenous amendments of various kinds. Walker *et al.* (1955) grew western redcedar in culture supplied with nitrogen at rates of 1.05 and 105 ppm and with phosphorus at 1.55 and 15.5 ppm. The foliar concentrations of nitrogen and phosphorus, calculated as $PO_4$, at the high levels were 2.94 and 1.09 percent, respectively, compared to 1.75 and 0.41 percent at the low levels.

Tamm (1956) decided that Scotch pine stands were deficient in nitrogen when the nitrogen in the needles was in the range of 1.1 to 1.6 percent and phosphorus was less than 0.10 percent. He found that phosphorus concentration in the foliage did not exceed 0.18 percent even in fertilized stands. In another trial with Scotch pine, Leyton and Armson (1955) found a significant correlation between height growth of the trees and nitrogen and phosphorus concentration in the terminal foliage. Nitrogen concentration varied from 1.26 to 1.76 percent and phosphorus from 0.14 to 0.21 percent dry weight. Leyton (1956) found also a significant relation between the amount of nitrogen and phosphorus in the foliage of Japanese larch (*Larix leptolepis* Murr.) and height growth.

Soluble phosphorus in the soil was directly related to seedling growth of eastern redcedar (*Juniperus virginiana* L.) in Arkansas. The concentration of phosphorus in the foliage of seedlings and of mature trees was related directly to the concentration of phosphorus in the soils (Fletcher and Ochrymowych, 1955).

Leaf and Keller (1956) found that on fertile soil the nitrogen and phosphorus concentrations of red pine foliage were 0.74 percent and 0.15 percent, respectively. The nitrogen concentration of vigorous, green Douglas-fir foliage was 1.1 to 1.7 percent compared with 0.6 to 0.8 percent for yellow foliage, according to Gessel and Walker (1956).

Differences in sampling procedures for foliar analysis may have caused differences in opinion as to the usefulness of foliar analysis. Leyton and Armson (1955) point out that the foliage of the terminal was most indicative of differences. In New Zealand, Will (1957) found that the nitrogen and phosphorus concentration in needles of Monterey pine (*P. radiata* D. Don.) varied with their age and their location in the crown. White (1954) sampled foliage of white and of red pine at monthly intervals at different locations on the tree. Nitrogen was highest in July, 1.45 percent, and was constant at about 1.20 percent during the fall and winter. Phosphorus remained at about 0.20 percent throughout the year. Nutrient contents were higher in the top of the crown than in the mid-crown.

In the absence of definitive data on the growth of pines in controlled conditions,

the study reported here was designed to provide information on the nutrition of loblolly and Virginia pines grown in a reproducible experimental system. Specifically the purposes of the study were: to investigate and compare the growth of loblolly and Virginia pine at various levels of nitrogen and of phosphorus; to determine sufficiency levels of these elements for the two pines; to relate foliar concentration of the two elements to the substrate level and to growth and development of the pines; and to compare the foliar concentration of the two elements under different levels of treatment with those found in trees in forests of various productivities.

## Materials and Methods

*Plant material.* One-year-old seedlings of loblolly and of Virginia pine were used. The loblolly pine seedlings had been grown in the Maryland State Forest Nursery, Harmans, Md., and the Virginia pine seedlings in flats in a greenhouse at the Plant Industry Station, Beltsville, Md. On the basis of a random sample of 30 trees, the average height of the loblolly seedlings was 10.4 cm. The dried tops and roots weighed 1.33 and 0.48 grams, respectively. The Virginia pine seedlings averaged 6.0 cm in height and the dried tops and roots weighed 0.94 and 0.97 gm, respectively. The nitrogen and phosphorus concentrations of the foliage, on a dry weight basis, were 1.40 and 0.22 percent for loblolly pine and 1.79 and 0.20 percent for Virginia pine, respectively.

*Design of the study.* To permit testing the significance of differences associated with treatments, the study was designed as a randomized block with three replications. Each replication contained 12 treatments of loblolly pine and 12 of Virginia pine. Six loblolly pine seedlings or six Virginia pine seedlings planted in a 5-gallon crock constituted a treatment unit. The crocks were filled with 18-mesh, white quartz sand which had been thoroughly washed with distilled water prior to the time of planting. The heights of all seedlings were measured after planting.

*Nutrient treatments.* The six levels of nitrogen and of phosphorus selected as treatments were 1, 5, 25, 100, 200, and 400 ppm. For all treatments in the nitrogen series, the phosphorus level was 100 ppm. For all treatments in the phosphorus series, the nitrogen level was 100 ppm. Phosphorus was added as mono-potassium phosphate through the 100 ppm phosphorus treatment and nitrogen was supplied as ammonium nitrate. Mono-sodium phosphate was used to increase phosphorus levels above 100 ppm. In this set of treatments the 100 ppm of nitrogen and the 100 ppm of phosphorus gave duplicate conditions. In order to provide a measure of the effect of the high sodium level used in the high phosphorus levels, the 100 ppm of phosphorus treatment was altered to receive the same concentration of sodium that the 400 ppm phosphorus treatment received. Concentrations of the macro-nutrients in the nutrient solutions are given in Table 1.

Iron was added at the rate of 1 ml of 0.5 percent ferric tartrate per liter of solution. Boron, as $H_3BO_4$, was added at the rate of 0.5 ppm; manganese, as $MnCl_2 \cdot 4H_20$, at 0.5 ppm; zinc, as $ZnSO_4 \cdot 4H_20$, at 0.05 ppm; copper, as $CuSO_4 \cdot 5H_20$, at 0.02 ppm; and molybdenum, as $H_2Mo0_4 \cdot H_20$, at 0.01 ppm.

The trees were irrigated at hourly intervals during the day with about 0.5 gallon of nutrient solution by means of the automatic irrigation system described by Gauch and Wadleigh (1943). Solutions were changed every three weeks and were adjusted each time to pH 5.5 with NaOH or HCl.

To keep the trees growing in the normally dormant period, daylight was extended to 15 hours by means of incandescent lights, following the observation of Kramer (1936).

*Harvesting and analyses.* The trees were grown for 50 weeks and were then measured and harvested. Full-grown needles from the terminals were collected separately from the other needles. Stems were cut from the roots at the sand line and the roots were carefully washed free of sand. Needles, stems, or roots of the trees in a pot were bulked to constitute a sample of the treatment. All fractions were dried 4-7 days at 70-80°C. The needle samples were ground in a Wiley mill to pass a 20-mesh screen and the roots and stems were passed through a hammer mill. Samples for analyses were oven-dried at 70-80°C. for 24 hours. All analyses are reported on an oven-dry weight basis.

Total nitrogen contents of foliage, stems, and roots were determined by the semi-micro Kjeldahl method as modified by Ranker (1927). Samples were analyzed in duplicate and were repeated if the difference between the duplicates was more than 5 percent of the average of the two values. For the phosphorus analyses samples were ashed with magnesium nitrate and treated with vanadate-molybdate reagent, as outlined by Richards (1954). The concentration of phosphorus was determined colorimetrically with a Bausch and Lomb colorimeter.

Potassium, sodium, and calcium contents of foliage were determined by flame photometry on a Beckman D U spectrophotometer. For these determinations two-gram samples of the foliage were dry-ashed at 525°C. for 12 hours and the ash was taken up in 10 ml of 1:1 hydrochloric acid. The solution was dried on a hotplate and the crystals were dissolved in 10 ml of 1:1 hydrochloric acid and the solution diluted with distilled water. After filtration the solution was made to 100 ml with distilled water. Aliquots of these solutions were diluted appropriately for the three cation determinations.

*Supplementary tests.* During the experiments, the growth of the pines in 1 ppm of phosphorus caused some doubt as to the actual phosphorus level and prompted a search for possible contamination. The question of reliability of the level brought

*TABLE 1. Concentrations of chemicals in the nutrient solutions used in the sand culture of loblolly and Virginia pines.*

| Nitrogen and phosphorus levels, ppm | Chemical | | | | | | |
|---|---|---|---|---|---|---|---|
| | $NH_4NO_3$ | $KH_2PO_4$ | $NaH_2PO_4$ | $MgSO_4$ | $CaCl_2$ | KCl | NaCl |
| | *Millimoles per liter* | | | | | | |
| 1 N | .0357 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 5 N | .1785 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 25 N | .8925 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 100 N | 3.57 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 200 N | 7.14 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 400 N | 14.28 | 3.23 | ...... | 1 | 1 | ...... | 1 |
| 1 P | 3.57 | .0323 | ...... | 1 | 1 | 3.1977 | 1 |
| 5 P | 3.57 | .1615 | ...... | 1 | 1 | 3.0685 | 1 |
| 25 P | 3.57 | .8075 | ...... | 1 | 1 | 2.4225 | 1 |
| 100 P | 3.57 | 3.23 | ...... | 1 | 1 | ...... | 10.69 |
| 200 P | 3.57 | 3.23 | 3.23 | 1 | 1 | ...... | 1 |
| 400 P | 3.57 | 3.23 | 9.69 | 1 | 1 | ...... | 1 |

to light the fact that the solutions were being contaminated by gravel used on top of the sand to inhibit growth of algae. Phosphorus levels in the solutions thought to contain 1 ppm phosphorus were found to vary from 2 to 4 ppm and the other levels were correspondingly 1 to 3 ppm higher. The leachate of 100 grams of gravel in 100 ml of 0.0001 molar nitric acid contained 2.5 ppm phosphorus. This concentration of acid was used to correspond with the acidity reached in the solutions at the end of a 3-week period—about pH 4.0.

As a result of finding that the low-phosphorus treatments, 1 ppm and 5 ppm, were substantially in error, another series of cultures was established. Again one-year-old loblolly and Virginia pine seedlings obtained from the Maryland State Forest Nursery were grown in sand culture. The average height and dry weight of the loblolly pines were 19.0 cm and 3.26 gm, and of the Virginia pines 13.0 cm and 1.87 gm, respectively. The needles of loblolly and Virginia pines contained 2.0 and 1.8 percent nitrogen, respectively, on a dry-weight basis. The phosphorus concentration in both species was 0.27 percent.

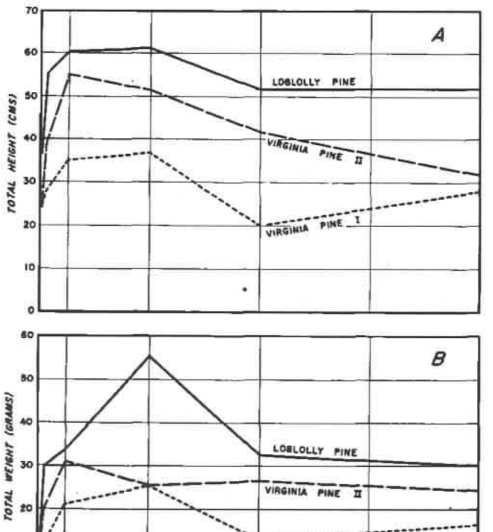


FIGURE 1. *A, Heights of loblolly pine trees and of Virginia pine trees (in two experiments) grown in sand culture with various levels of nitrogen. B, Total weights of the same test trees.*

Phosphorus treatment levels were 0, 0.1, 0.5, 1, and 5 ppm. Other nutrients were supplied at the same levels as in the previous test. The trees were planted January 27, 1957 and harvested October 13, 1957. The treatments were duplicated for each species. Plant material was handled as in the previous test. In addition, the nitrogen treatments, 1 to 400 ppm N, were repeated in duplicate with Virginia pine to check the response to nitrogen. Trees from the same lot as above were planted May 18, 1957, and harvested December 24. Plant material was treated as before.

For an estimate of the nitrogen and phosphorus content of foliage under natural conditions, foliage samples of loblolly pine were collected from two sites in Florida, 5 in Georgia, 5 in South Carolina, and 4 in Maryland. Virginia pine needles were collected from 5 sites in Maryland. Samples were obtained from the terminal growth of trees 3 to 5 feet high and were dried immediately after they were collected.

## Results and Discussion

### Growth

The growth of both pines showed a well-defined response for the levels of nitrogen and phosphorus in the nutrient solutions. This response was evident in the amount of growth, character of foliage, and morphology of the root system.

*Response to nitrogen.* Both pines responded to increased amounts of nitrogen up to a point beyond which additional nitrogen apparently was not used in growth. For height growth a sufficiency level was reached between 25 and 100 ppm nitrogen (Fig. 1, A). The difference in growth

between these two levels is not significant and the trends of the data do not suggest that an intermediate level would have resulted in a substantially greater height for either pine.

Total dry weight of loblolly pine was greatest in the 100 ppm nitrogen treatment (Fig. 1, B). This maximum weight was due to a larger amount of needles, since stem and root weights did not differ significantly from those in the 25 ppm nitrogen treatment.

The weights of the fractions of loblolly pine varied significantly with level of nitrogen. The weight of the needles was greater in the 100 ppm nitrogen treatment than in the 1, 5, 25, or 200 ppm nitrogen treatments (Table 2). The difference between the needle weights in the 100 and 400 ppm nitrogen treatments closely approached the 5 percent value arbitrarily set as the limit of significance. The weights of the stems and of the roots in the 100 ppm nitrogen treatment were significantly greater than the weights in the lowest and highest nitrogen levels.

The level of nitrogen did not affect the total weight of stems or of roots of Virginia pine. The weight of needles of trees grown in the 100 ppm nitrogen culture was greater than that of trees grown in the 1 or 5 ppm nitrogen culture.

The ratio of top to root weight appears to be controlled by the supply of nitrogen. This ratio increased about twofold from the lowest to the highest nitrogen treatments (Table 3). In the nitrogen experiment repeated with Virginia pine, the ratio was 1.20 for trees in the treatment with 1 ppm nitrogen and 3.98 for the 400 ppm nitrogen treatment. No trend existed in the phosphorus treatments in which the same amount of nitrogen was supplied.

The root systems showed marked differences in development as a result of the amount of nitrogen supplied. Under the higher nitrogen levels, as with 100 ppm, the lateral roots were long and fleshy and short roots were elongated. Moreover, the short roots were characterized by the presence of root hairs (Fig. 2). In the 1 and 5 ppm nitrogen treatments, roots were shorter, much less fleshy, and root hairs were absent. The short roots were conspicuously dichotomously branched or of coralloid branching habit (Fig. 2). These short roots were determined to be ectotrophic mycorrhizae.[2]

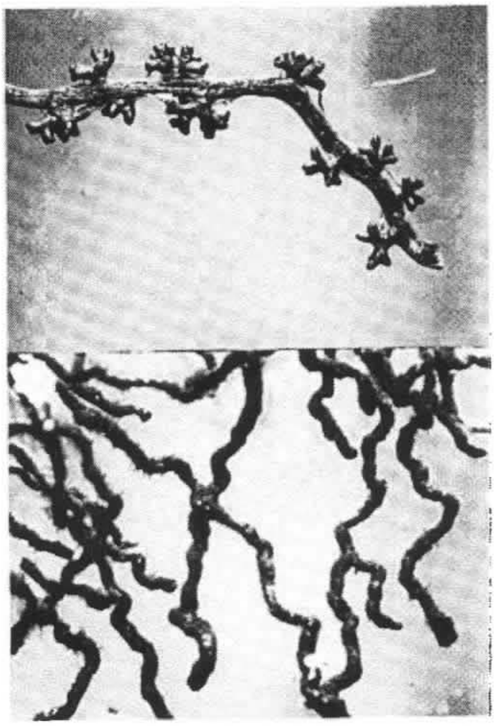

FIGURE 2. *At top, root of loblolly pine grown in sand culture with 1 ppm nitrogen, showing coralloid branching habit of mycorrhizal short roots. At bottom, roots of loblolly pine grown in sand culture with 100 ppm nitrogen, showing root hairs on long and short roots and lack of branching of short roots.*

[2]The presence and nature of the mycorrhizae was confirmed by Dr. Edward Hacskaylo, formerly with the Ornamental Crops Section, Agricultural Research Service, U. S. Dept. Agric., now with the Forest Service, Forest Physiology Laboratory, Beltsville, Md.

*TABLE 2. Average dry weights of fractions of loblolly and Virginia pines grown in sand culture with various levels of nitrogen and of phosphorus.*

| Nitrogen and phosphorus levels, ppm | Average dry weights of fractions, in grams | | | | | |
|---|---|---|---|---|---|---|
| | Loblolly pine | | | Virginia pine | | |
| | Needles[1] | Stems[2] | Roots[3] | Needles[4] | Stems[5] | Roots[5] |
| 1 N | 4.3 | 2.6 | 4.5 | 3.4 | 1.8 | 5.7 |
| 5 N | 12.4 | 6.8 | 10.6 | 4.4 | 2.3 | 5.3 |
| 25 N | 14.4 | 8.9 | 10.1 | 9.7 | 4.0 | 7.2 |
| 100 N | 27.8 | 12.7 | 15.1 | 13.3 | 3.9 | 8.2 |
| 200 N | 16.0 | 6.3 | 10.0 | 8.4 | 1.7 | 4.6 |
| 400 N | 17.3 | 5.6 | 7.1 | 8.6 | 2.4 | 5.3 |
| 1 P | 33.0 | 18.4 | 19.1 | 11.9 | 3.9 | 6.8 |
| 5 P | 25.3 | 17.3 | 15.5 | 9.3 | 3.3 | 6.5 |
| 25 P | 31.1 | 16.0 | 16.6 | 12.6 | 3.7 | 6.4 |
| 100 P | 34.4 | 17.7 | 16.1 | 12.1 | 4.4 | 6.6 |
| 200 P | 26.9 | 13.0 | 14.7 | 8.8 | 2.5 | 5.1 |
| 400 P | 21.2 | 8.8 | 11.8 | 8.4 | 2.4 | 5.6 |

[1]L.S.D. 5 percent, 11.8 gm; 1 percent, 18.1 gm.
[2]L.S.D. 5 percent, 6.8 gm; 1 percent, 9.3 gm.
[3]L.S.D. 5 percent, 6.1 gm; 1 percent, 8.3 gm.
[4]L.S.D. 5 percent, 5.5 gm; 1 percent, 7.5 gm.
[5]Treatments not significant.

Trees supplied with 1 or 5 ppm nitrogen showed definite symptoms of nitrogen deficiency. Needlles were short, stiff, and yellowish in color in contrast to the dark green of treatments with more nitrogen. In the highest nitrogen treatments, needles were very dark green and tended to be long and succulent. This was particularly noticeable with needles of Virginia pine on high nitrogen. These were 5-6 inches long with little resemblance to the stiff, short needles observed under natural conditions.

*Response to phosphorus.* The two pines grew well at low levels of phosphorus. The heights of both species in the treatment with 1 ppm phosphorus were significantly greater than or practically equal to the heights in the other phosphorus treatments (Table 4). The height of the loblolly trees supplied with 400 ppm phosphorus was significantly less than in the 5 and 25 ppm treatments. Inhibition was suggested in the Virginia pine but the differences were not significant at the 5 percent level. In the second experiment, at lower levels of phosphorus, height was definitely greater in the 1 ppm phosphorus treatment than in other treatments. Total dry weight of loblolly pine in the treatment with 1 ppm phosphorus was greater than, or approximately equal to, dry weights in the other treatments.

That loblolly and Virginia pines grew so well at low levels of phosphorus is not at all in agreement with the results of Mitchell (1939), which indicated that for white pine phosphorus was deficient at levels less than 50 ppm. These pines may actually have markedly different requirements, but differences in technique could explain the disparity in results. In the white pine study 27 trees were grown per pot and they were watered with slop culture only 2 or 3 times daily. Thus there may have been much more competition for phos-

phorus than in the current study with loblolly and Virginia pines. Some agricultural crops, such as corn, barley, and tomatoes grow very well with phosphorus levels below 1 ppm, provided the level is constantly maintained (Arnon, 1953). Cotton, however, has a higher requirement, growing only one tenth as much at 2.6 ppm as at 20 ppm phosphorus (Ergle and Eaton, 1957). Citrus trees also have a higher requirement, according to Chapman and Rayner (1951), who found that 2.5 to 3.5 ppm $PO_4$ was insufficient for citrus while 18-20 ppm resulted in healthy trees.

Early abscission of foliage, resulting in sparseness, was the only evidence of phosphorus deficiency in the current study. These symptoms were obvious in the treatment with 0 and 0.1 ppm phosphorus. The common symptom of phosphorus deficiency in pines, purplish foliage, was not evident.

Phosphorus level also affected the morphology of the roots. In the treatments with 0, 0.1, and 0.5 ppm phosphorus, both species had short roots which were conspicuously dichotomously branched. This is typical of mycorrhizal formation. In the 1 ppm phosphorus treatment there were a few branched short roots. The unbranched short roots were without root hairs in loblolly but with root hairs in Virginia pine. At levels of 5 ppm phosphorus and higher, mycorrhizal short roots were nonexistent or scarce on both species and root hairs were profuse.

The occurrence of mycorrhizae on roots of trees supplied with low levels of phosphorus and nitrogen is in agreement with the findings of Hatch (1937). He concluded that mycorrhizae would be present on tree roots whenever certain inorganic nutrients such as phosphorus, nitrogen, and potassium were present in low concentrations and that they would not be present in very fertile soils or adequately supplied cultures.

If it is assumed that root systems bearing mycorrhizae are desirable in forest planting

*TABLE 3. Top/root ratios, dry weight basis, of loblolly and Virginia pines grown in sand culture with various levels of nitrogen and of phosphorus.*

| Nitrogen and phosphorus levels, ppm | Top/root ratio Loblolly pine | Virginia pine |
|---|---|---|
| 1 N | 1.53 | 0.91 |
| 5 N | 1.81 | 1.30 |
| 25 N | 2.30 | 1.90 |
| 100 N | 2.68 | 2.10 |
| 200 N | 2.23 | 2.20 |
| 400 N | 3.22 | 1.89 |
| 1 P | 2.70 | 2.30 |
| 5 P | 2.76 | 2.02 |
| 25 P | 2.78 | 2.54 |
| 100 P | 3.23 | 2.50 |
| 200 P | 2.70 | 2.22 |
| 400 P | 2.54 | 1.83 |

*TABLE 4. Heights and total dry weights of loblolly and Virginia pine trees grown in two sand culture experiments with various levels of phosphorus.*

| Phosphorus level (ppm) | Height Loblolly (cm) | Virginia (cm) | Total dry weight Loblolly (gm) | Virginia (gm) |
|---|---|---|---|---|
| | EXPERIMENT I | | | |
| 1 | 68.8[1] | 35.0[2] | 70.5[3] | 22.5[4] |
| 5 | 74.9 | 30.0 | 59.7 | 19.1 |
| 25 | 72.5 | 31.9 | 62.1 | 22.8 |
| 100 | 69.8 | 33.7 | 68.3 | 23.1 |
| 200 | 65.7 | 28.4 | 54.6 | 16.4 |
| 400 | 59.9 | 27.2 | 41.4 | 15.1 |
| | EXPERIMENT II | | | |
| 0 | 54.0 | 61.6 | 25.6 | 18.6 |
| 0.1 | 70.5[5] | 67.4[5] | 63.0[6] | 48.0[6] |
| 0.5 | 76.0 | 67.4 | 68.4 | 59.3 |
| 1.0 | 97.4 | 81.6 | 72.3 | 63.7 |
| 5.0 | 71.9 | 73.0 | 72.5 | 76.0 |

[1]L.S.D. 5 percent, 11.9; L.S.D. 1 percent, 16.2.
[2]L.S.D. 5 percent, 9.0; L.S.D. 1 percent, 12.2.
[3]L.S.D. 5 percent, 23.2; L.S.D. 1 percent, 32.9.
[4]Difference not significant.
[5]L.S.D. 5 percent, 8.4; L.S.D. 1 percent, 12.5.
[6]Differences not significant if 0 level data omitted from analysis.

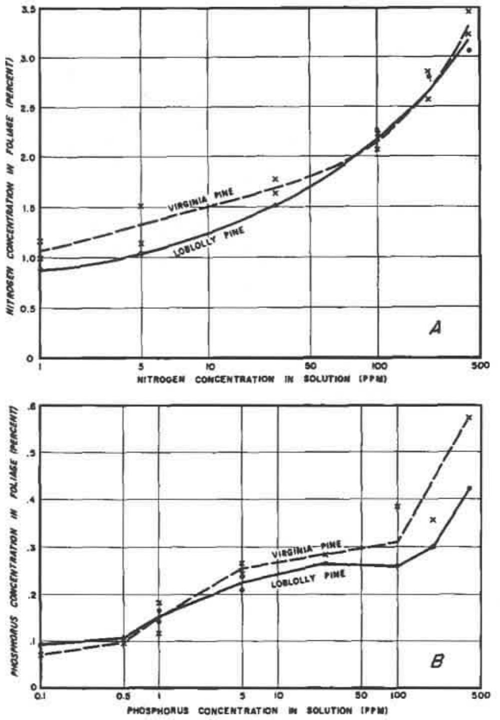


FIGURE 3. *A. The relation of nitrogen concentration in the upper foliage of loblolly and Virginia pines to nitrogen concentration in the nutrient solution. B, Similar relation with respect to phosphorus concentrations.*

stock, the existence of mycorrhizae only at low levels of nitrogen and phosphorus is significant for forest nursery practice. The low top/root ratios in the trees at low nitrogen levels are also significant. Over-fertilization of forest nurseries thus could produce topheavy trees with undesirable roots.

*Response to sodium.* Although the effect of sodium level was a minor part of the study, some data were derived from the study of phosphorus levels. Sodium was added to the 100 ppm phosphorus treatment to equal the total sodium concentration of the 400 ppm phosphorus treatment. Loblolly and Virginia pines were not inhibited by the amount of sodium added—10.69 millimoles per liter or 246 ppm. In fact, both height growth and total dry weight of the two pines were essentially as good in this treatment as in any other (Table 4). Thus the apparent depression of growth at the highest level of phosphorus was not caused by the added sodium. It is still a question as to whether or not sodium is an essential element. However, the concentration of sodium in the other nutrient solutions was equal to that used by Wooley (1957)—one millimole of NaCl per liter—who obtained a 12 percent gain in yield of tomatoes over solutions with no added sodium.

### Uptake of Nutrients

The concentrations of nitrogen and of phosphorus in the needles, stems, and roots were directly related to the concentrations of the elements in the nutrient solution.

*Nitrogen uptake.* The concentration of nitrogen in the upper needles of loblolly pine varied from 0.88 percent in the treatment with 1 ppm nitrogen to 3.06 percent in the treatment with 400 ppm nitrogen. For the same levels in the nutrient solution, the concentration of nitrogen in the upper needles of Virginia pine was 1.16 and 3.46 percent, respectively. These trends are shown in Figure 3, A. The nitrogen concentration in the remainder of the needles was slightly higher, varying from 0.94 to 3.94 percent in loblolly pine and 1.17 to 3.75 percent in Virginia pine (Table 5).

In the phosphorus treatments, each of which received the same amount of nitrogen, the concentration of nitrogen in the foliage was practically constant, with one exception. The nitrogen concentration of the foliage of loblolly pine in the treatment with 1 ppm phosphorus was significantly lower than that of the other treatments. Shear, *et al.* (1948) observed that in tung trees with uniform nitrogen supply the nitrogen concentration was depressed in treatments given low dosages of phosphorus. Two possible explanations are:

*TABLE 5. Nitrogen concentration in needles, stems, and roots of loblolly and Virginia pine grown in sand cultures with various levels of nitrogen and phosphorus.*

| Nitrogen and phosphorus levels, ppm | Nitrogen concentration in dry material, in percent | | | | | |
|---|---|---|---|---|---|---|
| | Loblolly pine | | | Virginia pine | | |
| | Needles[1] | Stems[2] | Roots[3] | Needles[1] | Stems[2] | Roots[3] |
| 1 N | 0.94 | 0.27 | 0.53 | 1.17 | 0.69 | 0.89 |
| 5 N | 1.24 | .34 | .73 | 1.39 | .91 | 1.56 |
| 25 N | 1.73 | .56 | 1.17 | 1.88 | 1.00 | 2.03 |
| 100 N | 2.32 | .92 | 2.02 | 2.30 | 1.13 | 2.24 |
| 200 N | 2.71 | 1.20 | 2.64 | 3.12 | 1.68 | 2.59 |
| 400 N | 3.94 | 1.58 | 2.93 | 3.75 | 2.01 | 3.19 |
| 1 P | 1.81 | .63 | 1.22 | 2.57 | 1.22 | 2.34 |
| 5 P | 2.24 | .81 | 1.46 | 2.40 | 1.12 | 1.86 |
| 25 P | 2.36 | 1.04 | 1.89 | 2.38 | 1.26 | 2.23 |
| 100 P | 2.12 | .81 | 1.48 | 2.38 | 1.16 | 1.79 |
| 200 P | 2.31 | .92 | 2.11 | 2.31 | 1.24 | 2.29 |
| 400 P | 2.23 | .92 | 2.29 | 2.51 | 1.28 | 2.11 |

[1]L.S.D. 5 percent, 0.49; L.S.D. 1 percent, 0.65.
[2]L.S.D. 5 percent, 0.27; L.S.D. 1 percent, 0.35.
[3]L.S.D. 5 percent, 0.45; L.S.D. 1 percent, 0.60.

*TABLE 6. Phosphorus concentration in needles, stems, and roots of loblolly and Virginia pine grown in sand culture with various levels of nitrogen and phosphorus.*

| Nitrogen and phosphorus levels, ppm | Phosphorus concentration in dry material, in percent | | | | | |
|---|---|---|---|---|---|---|
| | Loblolly pine | | | Virginia pine | | |
| | Needles[1] | Stems[2] | Roots[3] | Needles[1] | Stems[2] | Roots[3] |
| 1 N | 0.621 | 0.179 | 0.419 | 0.743 | 0.241 | 0.460 |
| 5 N | .446 | .164 | .448 | .612 | .231 | .408 |
| 25 N | .381 | .153 | .376 | .504 | .219 | .432 |
| 100 N | .286 | .171 | .376 | .435 | .191 | .380 |
| 200 N | .289 | .159 | .389 | .568 | .215 | .359 |
| 400 N | .349 | .185 | .286 | .415 | .193 | .254 |
| 1 P | .179 | .082 | .123 | .175 | .147 | .203 |
| 5 P | .222 | .106 | .156 | .292 | .177 | .255 |
| 25 P | .266 | .153 | .290 | .331 | .171 | .317 |
| 100 P | .268 | .147 | .274 | .450 | .182 | .331 |
| 200 P | .340 | .188 | .395 | .478 | .216 | .390 |
| 400 P | .486 | .204 | .530 | .943 | .308 | .520 |

[1]L.S.D. 5 percent, 0.147; L.S.D. 1 percent, 0.196.
[2]L.S.D. 5 percent, 0.042; L.S.D. 1 percent, 0.156.
[3]L.S.D. 5 percent, 0.068; L.S.D. 1 percent, 0.091.

(1) that low phosphorus resulted in less energy available for active uptake of the nitrate and possibly the ammonium, and (2) that low phosphorus supply reduced the synthesis of chloroplastic, cytoplasmic, and nuclear proteins in the foliage. Nitrogen concentrations in the stems and roots were lower than in the needles but followed the same trends (Table 5). On the average, nitrogen concentration was higher in Virginia than in loblolly pine in the same treatments.

Both loblolly and Virginia pine used practically all the nitrogen supplied in the 1 ppm treatment, a total of 0.3 gm during the experiment. The nitrogen in the 6 loblolly trees per pot amounted to 0.427 gm, based on the weights of the fractions and the nitrogen concentration in each fraction. The trees contained 0.153 gm at the time they were planted. This plus the 0.3 gm supplied in the culture accounts for the nitrogen content of the trees. The original amount in Virginia pine, 0.205 gm, plus the added 0.30 gm, is very close to the 0.514 gm found in 6 Virginia pine trees in the 1 ppm nitrogen treatment. In the second experiment with Virginia pine the 6 trees contained 0.151 gm nitrogen at the start of the test and were given 0.175 for a total of 0.326 gm. At the end of the experiment, 6 trees contained 0.315 gm. In the treatment with 5 ppm nitrogen, the 1.5 gm nitrogen supplied plus the original amount exceeded only slightly the amount found in the 6 trees. In Virginia pine the total amount found was 0.998 gm compared to a total supply of 1.705 gm. In the second experiment with Virginia pine, 6 trees in the 5 ppm nitrogen treatment obtained 0.796 gm of nitrogen from a supply of 0.875 gm. At higher concentrations the trees used progressively less of the amounts supplied. For loblolly pine, in treatments with 25, 100, 200, and 400 ppm nitrogen, the trees absorbed 26, 21, 7.5, and 4.8 percent of the nitrogen, respectively.

*Phosphorus uptake.* The concentration of phosphorus in the upper needles of loblolly and Virginia pine varied from 0.164 and 0.181 percent, respectively, in the 1 ppm phosphorus treatment, to 0.422 and 0.572 percent, respectively, in the 400 ppm phosphorus treatment. In the second experiment with phosphorus the percentages of phosphorus in the needles in the 1 ppm treatment were 0.145 and 0.112, respectively, for loblolly and Virginia pine. The trend of concentration of phosphorus in the needles is shown in Figure 3, B. Phosphorus concentrations in the stems and roots were lower than in the needles but followed the same trends (Table 6).

The percentage of phosphorus in the needles in the treatment with 1 ppm nitrogen was significantly greater than in treatments with greater amounts of nitrogen. This may be interpreted as resulting from decreased competition between the nitrate and phosphate ions. Van Goor (1953), working with larch, suggested that there was antagonism between nitrogen and phosphorus with nitrogen decreasing the uptake of phosphorus, and vice versa. This conclusion is not completely borne out by the results in the nitrogen series, where low phosphorus resulted in low nitrogen uptake. Another possible interpretation of the higher phosphorus concentration is the same amount of phosphorus being distributed in less dry material.

The total amounts of phosphorus in the loblolly and Virginia pine trees in the 1 ppm phosphorus treatment were 0.586 and 0.242 gm, respectively, compared with the 0.3 gm supplied in the culture solution plus an initial amount of 0.024 and 0.023 gm, respectively, in the two species. Contamination from the gravel, and perhaps other sources, apparently supplied the difference between the 0.562 gm taken up by the 6 loblolly trees and the 0.3 gm available in the culture solution. In the second experiment with phosphorus the total amount of phosphorus also exceeded

that which could be accounted for, since the loblolly trees apparently took up 0.403 gm whereas only 0.225 gm was added during the experiment. Closer correspondence was found in the Virginia pines which obtained 0.310 gm from a supply of 0.225 gm. In the 5 ppm treatment, loblolly and Virginia pines took up 0.565 gm and 0.275 gm, respectively, in the first experiment, and 0.735 gm and 0.766 gm, respectively, in the second experiment. The total supply was 1.5 gm in the first experiment and 1.125 in the second. Uptake was relatively lower in the treatments with more phosphorus, being only 12, 3.2, 1.7, and 0.9 percent for loblolly pine in the 25, 100, 200, and 400 ppm phosphorus treatments and 4.5, 1.6, 1.0, and 0.6 percent for Virginia pine in the same treatments. In the treatments given less than 1 ppm phosphorus, more phosphorus was found in the plant than could be accounted for on the basis of the initial amount plus that added. There apparently was contamination in these low levels, such as from the distilled water or dust blown in from outside.

*Uptake of sodium, potassium, and calcium.* Trees in the treatment in which sodium was supplied in highest amounts contained much more sodium than in the other treatments (Table 7). The concentration of sodium in the foliage of trees in the 100 and 400 ppm phosphorus treatments, both of which were supplied with sodium at the rate of 244 ppm, was from 0.124 to 0.322 percent. All other treatments received sodium at the rate of 23 ppm with the exception of the 200 ppm phosphorus treatment, in which the rate was 97 ppm. In all of the nitrogen treatments the sodium concentration in the foliage was from 0.044 to 0.085 percent.

The percentages of potassium in trees in the 1 and 5 ppm nitrogen treatments was significantly higher than in all other treatments except in those given 100 ppm phosphorus with additional sodium (Table 7). The higher concentration in the low nitrogen treatments might be explained on the basis of the lesser growth of trees in these treatments. The foliage in the 1 and 5 ppm nitrogen treatments contained 0.055

*TABLE 7. Concentration of sodium, potassium, and calcium in the foliage of loblolly and Virginia pines grown in sand culture with various nitrogen and phosphorus levels.*

| Nitrogen and phosphorus levels, ppm | Concentration, in percent | | | | | |
|---|---|---|---|---|---|---|
| | Loblolly pine | | | Virginia pine | | |
| | Na | K | Ca | Na | K | Ca |
| 1 N | 0.067 | 1.28 | 0.25 | 0.073 | 1.02 | 0.24 |
| 5 N | .076 | 1.14 | .17 | .069 | .92 | .25 |
| 25 N | .062 | 1.07 | .10 | .050 | .78 | .22 |
| 100 N | .057 | .96 | .12 | .060 | .64 | .19 |
| 200 N | .079 | .79 | .11 | .046 | .69 | .19 |
| 400 N | .085 | 1.01 | .12 | .044 | .58 | .18 |
| 1 P | .074 | .85 | .14 | .051 | .64 | .19 |
| 5 P | .085 | 1.07 | .19 | .058 | .54 | .22 |
| 25 P | .059 | 1.04 | .13 | .048 | .80 | .19 |
| 100 P | .129 | .95 | .15 | .210 | 1.12 | .22 |
| 200 P | .072 | .93 | .13 | .043 | .64 | .19 |
| 400 P | .322 | .91 | .09 | .263 | .76 | .16 |

gm of potassium compared, for example, with 0.154 gm in the 25 ppm nitrogen treatment.

The concentration of calcium also was highest in the low nitrogen treatments, but here also the total uptake of calcium was less than in other treatments. The percentage of calcium in trees was more or less constant in the phosphorus treatments. Competition between calcium, potassium, and sodium and the ammonium ion may be in effect here, but the observed differences in concentration are probably the result of differences in weight.

*Relation of foliar concentration of nitrogen and phosphorus to growth.* The concentration of nitrogen in foliage of loblolly and Virginia pines with the best growth varied from 1.7 to 2.3 percent. Growth was limited when the nitrogen concentration in the foliage was 1.2 percent or less, and foliar concentration over 2.3 percent indicated luxury consumption. These data agree with the findings of Leyton and Armson (1955) in that increased growth was accompanied by increased nitrogen concentration in the foliage up to the sufficiency level. The trend is not linear because with luxury consumption of nitrogen, growth decreased. Gessel, *et al.* (1950) noted that on the best sites the nitrogen concentration in Douglas-fir needles was 2.1 percent, and Tamm (1956) concluded that a foliar concentration of 1.1 to 1.6 percent indicated a deficiency.

Best growth of the trees in the phosphorus culture series was coincident with a phosphorus concentration of 0.14 to 0.18 percent in the foliage. In some treatments of loblolly pine, the phosphorus concentrations were as high as 0.62 percent. Less than about 0.10 percent may represent a deficiency. A similar level of phosphorus deficiency was indicated by Tamm for Scotch pine.

*Nitrogen and phosphorus in forest trees.* The nitrogen concentration in the foliage of loblolly pines in forests varied from 0.87 to 1.52 percent. A difference of 0.11 percent between locations was significant at the 5 percent level. Significant differences with respect to phosphorus concentration in loblolly needles were also found among the 16 sample locations. The phosphorus concentrations varied from 0.089 to 0.167 percent and a difference of 0.016 percent was significant at the 5 percent level.

The average concentration of nitrogen and phosphorus in the foliage of Virginia pine varied from 1.19 to 1.33 percent and 0.122 to 0.158 percent, respectively, by locations. On 4 sites where Virginia and loblolly pines were intermingled, there was little difference between the two species with respect to foliar concentration of nitrogen or phosphorus. The average concentration of nitrogen and of phosphorus in loblolly pine foliage was 1.20 and 0.148 percent, respectively, compared with 1.26 and 0.140 percent in Virginia pine foliage.

On the basis of these data and that from the trees grown in culture, it appears that loblolly and Virginia pines differ little with respect to their efficiency in absorbing nitrogen and phosphorus. At the levels of nitrogen and of phosphorus which were deficient for growth, both pines accumulated all or nearly all the nitrogen and phosphorus available. At higher levels where there was "luxury" consumption, the concentration of nitrogen and phosphorus was greater in Virginia pine but the total uptake was less. With respect to requirements for nitrogen and phosphorus these two pines have equal ability to exist on poor soils.

The foliar analyses of trees growing on a variety of sites indicate that some areas are deficient with respect to available nitrogen and phosphorus, and suggest the need of field tests to determine the feasibility of fertilizing with these elements.

## Conclusions

On the basis of this study of the growth of loblolly and Virginia pines supplied with various levels of nitrogen and phosphorus

in sand culture, plus supplementary information from naturally grown trees, the following conclusions may be drawn:

1. Both loblolly and Virginia pine grow best when nitrogen is supplied at a constant rate of from 25 to 100 ppm. Inasmuch as there was so little difference in response between the two levels, nitrogen at 25 ppm or a value between 25 and 100 may be assumed to represent a sufficiency level.

2. A constant supply of 1 ppm of phosphorus is adequate for the growth of the two pines.

3. There is no evidence of a difference between the two pines with respect to their requirements for nitrogen and phosphorus. Availability of these elements thus is not a deciding factor in the competition between these two pines on a given site.

4. A concentration of 1.7 to 2.3 percent nitrogen and 0.14 to 0.16 percent phosphorus in the foliage of these two pines indicates satisfactory nutrition with these elements.

5. Nitrogen deficiency is indicated by short, stiff, yellowish-green needles.

6. Phosphorus deficiency is indicated by early abscission of the needles in trees 1 to 2 years old. There may have been a translocation of phosphorus to growing points which prevented the appearance of the purplish color frequently observed on the tips of young phosphorus-deficient pine seedlings.

7. The presence of mycorrhizae may indicate a deficiency of nitrogen or phosphorus.

8. Sodium, as high as 250 ppm, does not adversely affect the growth or development of these pines.

9. Judging by these data, the growth of some of the trees sampled under natural forest conditions is probably limited by deficiencies of nitrogen or phosphorus.

### Summary

One-year-old loblolly and Virginia pine seedlings were grown in automatically irrigated sand culture for 50 weeks to study their response to various levels of nitrogen and phosphorus. A randomized block design with 3 replications of each treatment was employed. The treatment levels of phosphorus and of nitrogen were 1, 5, 25, 100, 200, and 400 ppm and 0, 0.1, and 0.5 ppm phosphorus in a supplementary study. Other macro- and micro-elements were supplied in concentrations commonly used in nutrient cultures and in the same amounts for all treatments. Six seedlings were grown in each pot of sand. The seedlings were irrigated hourly each day from 0700 to 2100. A day length of 15 hours was insured during the fall and winter by incandescent lamps to extend the growing season. When the seedlings were harvested, full-grown needles from the terminal were collected separately from the remainder of the needles. The stem and root were separated at the sand line. All plant parts were immediately dried for several days at 70° C. Heights of the seedlings and dry weights of the plant fractions were measured. For an estimate of the concentration of nitrogen and phosphorus under forest conditions, needle samples of loblolly pine were obtained from 16 locations and of Virginia pine from 5 locations.

The concentration of nitrogen and of phosphorus was determined in the needles, stems, and roots of the plants grown in culture, and in the needle samples from the forested areas. The semi-micro Kjeldhal technique was used for determinations of total nitrogen. The molybdate-vanadate reagent was used for colorimetric determination of phosphorus content. The amounts of sodium, potassium, and calcium in the needles were determined with the flame spectrophotometer.

With respect to nitrogen, maximum growth of the pines occurred in the treatments with 25 and 100 ppm nitrogen. The sufficiency level lies between these two concentrations. A substrate concentration of 1 ppm phosphorus was adequate for growth. There is no evidence of a difference between loblolly and Virginia pines

with respect to their requirements for nitrogen and phosphorus.

The symptoms of nitrogen deficiency. apparent in the treatments with 1 and 5 ppm nitrogen, were short, stiff needles of yellowish-green color. Early abscission of the needles in treatments with none and 0.1 ppm phosphorus indicated phosphorus deficiency. Both loblolly and Virginia pine exhibited luxury consumption of nitrogen and phosphorus. The concentration of these elements in the foliage increased with the amount supplied in the culture solution.

In the trees making the best growth, the nitrogen concentration in the terminal needles varied from 1.7 to 2.3 percent. The phosphorus concentration of terminal needles in the fastest-growing trees, supplied with 1 ppm phosphorus, was between 0.14 to 0.16 percent. A nitrogen concentration of less than 1.2 percent and a phosphorus concentration of less than 0.10 percent were found in the needles of trees deficient in these elements.

The concentration of nitrogen in the needles of loblolly pine trees from various locations varied from 0.87 to 1.52 percent; the phosphorus concentration varied from 0.09 to 0.17 percent. For Virginia pine these values were 1.19 to 1.33 percent and 0.12 to 0.16, respectively.

Mycorrhizae were found on the roots of loblolly and Virginia pines which were supplied with insufficient amounts of nitrogen or phosphorus.

The study points out possible deficiencies of nitrogen and phosphorus under forest conditions and provides a basis for additional studies of the inorganic nutrition of pines.

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